VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 1: 7–20
doi: 10.3897/VCS/2020/37980

RESEARCH PAPER

Forest characteristics, population structure and growth trends of *Pinus yunnanensis* in Tianchi National Nature Reserve of Yunnan, southwestern China

Cindy Q. Tang[1], Li-Qin Shen[1], Peng-Bin Han[1], Diao-Shun Huang[1], Shuaifeng Li[2], Yun-Fang Li[3], Kun Song[4], Zhi-Ying Zhang[1], Long-Yun Yin[5], Rui-He Yin[5], Hui-Ming Xu[5]

1 *Institute of Ecology and Geobotany, College of Ecology and Environmental Science, Yunnan University, Yunnan, China*
2 *Research Institute of Resource Insects, Chinese Academy of Forestry, Yunnan, China*
3 *Forest Station of Yunlong Forestry Bureau, Yunnan, China*
4 *School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China*
5 *Management Office of Tianchi National Nature Reserve, Yunnan, China*

Corresponding author: Cindy Q. Tang (cindyqtang@aol.com); Shuaifeng Li (12704391@qq.com)

Academic editor: David W. Roberts ♦ **Received** 4 July 2019 ♦ **Accepted** 1 September 2019 ♦ **Published** 4 May 2020

Abstract

Aims: *Pinus yunnanesis* is commercially, culturally and economically important, but there is a lack of ecological data on its role in stand dynamics. Our aims are to clarify the structure, composition, regeneration and growth trends of primary mature *P. yunnanensis* forests. **Study area:** The Tianchi National Nature Reserve in the Xuepan Mountains, Yunlong County, northwestern Yunnan, China. **Methods**: We investigated forests containing *P. yunnanensis*, measured tree ages and analyzed the data. **Results:** Six forest types were identified: (1) coniferous forest: *Pinus yunnanensis* (Type 1); (2) mixed coniferous and evergreen broad-leaved forest: *P. yunnanensis-Lithocarpus variolosus* (Type 2); (3) mixed coniferous and deciduous broad-leaved forest: *P. yunnanensis-Quercus griffithii* (Type 3); (4) mixed evergreen broad-leaved and coniferous forest: *Castanopsis orthacantha-P. yunnanensis-Schima argentea* (Type 4); (5) mixed coniferous, evergreen and deciduous broad-leaved forest: *Pinus yunnanensis-Schima argentea-Quercus griffithii* (Type 5); (6) mixed coniferous and evergreen broad-leaved forest: *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* (Type 6). The size- and age-structure and regeneration patterns of *P. yunnanensis* were highly variable within these six forest types. *P. yunnanensis* regeneration was well balanced in forest Type 1 as compared to the other five types. All six forest types were identified as rare and old-growth with *P. yunnaensis* trees reaching ages of more than 105 years (a maximum age of 165 years with a diameter 116 cm at breast height) except for the Type 4 forest (a 90-year-old stand). Growth rates of *P. yunnanensis*, based upon ring width measurements, were high for the first 10 years, then declined after the 10th year. In contrast, basal area increment (BAI) increased for the first 25 years, plateaued, and only declined as trees became older. Trees in the older age classes grew more quickly than younger trees at the same age, a consequence of either site quality or competitive differences. The BAI of *P. yunnanensis* in all age classes in the Tianchi National Nature Reserve was much higher than those of the secondary and degraded natural *P. yunnanensis* forests of other areas. **Conclusions:** The *P. yunnanensis* forests of the Tianchi area appear to be some of the last remnants of primeval and old-growth forests of this species. These forests are structurally diverse and contain a rich diversity of overstory, mid-story, and understory species.

Taxonomic reference: Editorial Committee of Flora Republicae Popularis Sinicae (1959–2004) for vascular plants.

Abbreviations: BA = basal area; BAI = basal area increment; DBH = diameter at breast height; H = height; RBA = relative basal area.

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Keywords

Age-class, basal area increment, forest stratification, growth rate, old-growth forest, regeneration pattern, species diversity

Introduction

In East Asia, warm-temperate pines (e.g., *Pinus yunnanensis, P. kesiya, P. massoniana, P. taiwanensis, P. roxburghii, P. thunbergii*) grow mainly at low to mid-high elevations on dry or humid mountain slopes, cliffs, rock barrens, or ridges. They also grow in valleys and on disturbed sites in subtropical and warm-temperate areas. Temperate/cold-temperate pines (e.g., *P. densata*, *P. wallichiana*, *P. pumila*) occur at high elevations or in cold locations, being able to withstand cold and snow. Warm-temperate species of *Pinus* often form a mosaic of stand structures across the landscape of subtropical China (Tang 2015). *P. yunnanensis* (Yunnan pine) is native to subtropical southwestern China at 400–3,100 m above sea level (m a.s.l.), but mainly between 1,600–2,900 m ranging 23°–30°N and 96°–108°E (Jin and Peng 2004; Chen et al. 2012; http://www.eFloras.org). The more northern ecological partner, *Pinus tabuliformis,* is widely distributed at 100–2,600 m ranging 31°N–44°N, 101°30'E–124°25'E in temperate areas of China and Korea. The southern ecological partner, *Pinus kesiya,* is found at mainly 700–1,800 m in southeastern Tibet, southern Yunnan, northeastern India, Laos, Myanmar, Philippines, Thailand, Vietnam (Xu 1990; Wen et al. 2010; http://www.eFloras.org). In many localities *P. yunnanensis* occurs in almost pure stands. In the subtropical zone, *P. yunnanensis* is often found in early or intermediate-successional stands after destruction of the evergreen broad-leaved forest by human activities or after forest fires (Tang 2015). In general forest stands of *P. yunnanensis* present a young age structure (Wang et al. 2018). Old-growth or primary mature *P. yunnanensis* forests are now confined to a very few nature reserves in Yunnan and southeastern Tibet.

P. yunnanesis is commercially (resin and timber), culturally and economically important, but there is a lack of ecological data on its role in succession and stand dynamics. There are studies on *P. yunnanensis* community succession after fire (Tang et al. 2013), seed germination following fire (Su et al. 2017), seedling growth under experimental conditions (Cai et al. 2016), regeneration in plantations (Wang et al. 2017), secondary growth forests, degraded and restored forests in central Yunnan (e.g., Chen and An 1993; Peng et al. 2005, 2012; Shi et al. 2009; Yang 2010), as well as its genetics (e.g., Yu et al. 2000; Xu et al. 2011; Wang et al. 2013). However, studies of forest stand characteristics including species diversity, size and age structure, as well as growth rates of the old-growth *P. yunnanensis* forest are not available. Li et al. (2007) identified a *P. yunnanensis* forest in Yongren, central Yunnan as an old-growth forest with trees having a maximum DBH of 48 cm and a corresponding age of 257 years, but they did not provide data on ring width and did not explain how they collected age data. In addition, no information regarding stand characteristics was provided. An understanding of forest features and population structure of old-growth forests is crucial for gene bank and biodiversity conservation.

The Tianchi National Nature Reserve of Yunnan is designated to protect old-growth and primary mature forests dominated by *P. yunnanensis*. The Reserve affords a unique opportunity to study *P. yunnanensis* over a wide range of elevations, forest types, and age classes, including old-growth forest stands. We address the following questions: What are the structural features of forests containing *P. yunnanensis* in the Tianchi National Nature Reserve? What are the population structure and regeneration patterns of this species? What are the growth trends in the study area based upon ring area and width data?

Methods

Study area

The Tianchi National Nature Reserve is located in the subtropical zone of Yunnan between an elevation range of 2,100 to 3,226 m The Reserve includes Tianchi and Longmashan areas in the Xuepan Mountains, Yunlong County, northwestern Yunnan, China (Figures 1a, b).

The mountain slopes of our study area have the red or yellow-reddish soil in 2,100–2,300 m elevation zone, the yellow-brown soil in 2,300–2,700 m zone and the brown soil in 2,700–3,200 m zone (Su et al. 2013). The water content of surface soil is 16.7% on average, ranging from 9.6% to 21.4% at 2,500–2,700 m (Jin and Peng 2004). It is characterized by a subtropical, humid climate that is largely controlled by the summer monsoon of India and the East Asian summer monsoon. The temperature lapse rate with elevation is 0.56 °C /100 m (Su and Wang 2013). The mean annual temperature is 13.8 °C at 2,000 m and 7.1 °C at 3,200 m with a warm month mean of 19.7 °C at 2,000 m and 13.4 °C at 3,200 m in June and a cold month mean of 6.5 °C at 2,000 m and 0.3°C at 3,200 m in January. The mean annual precipitation is 975.1 mm at 2,000 m and 1,313.5 mm at 3,200 m, of which about 80% falls between March and October. The monthly relative humidity is greater than 85%.

Study species

The focal species of this study is *P. yunnanensis* (Figures 2a–e). *P. yunnanensis* is an evergreen coniferous species that can grow to mature heights over 30 m, or assume shrub-like forms in extremely dry habitats. Needles are 2 or 3 per bundle. Seed cones shortly pedunculate, green,

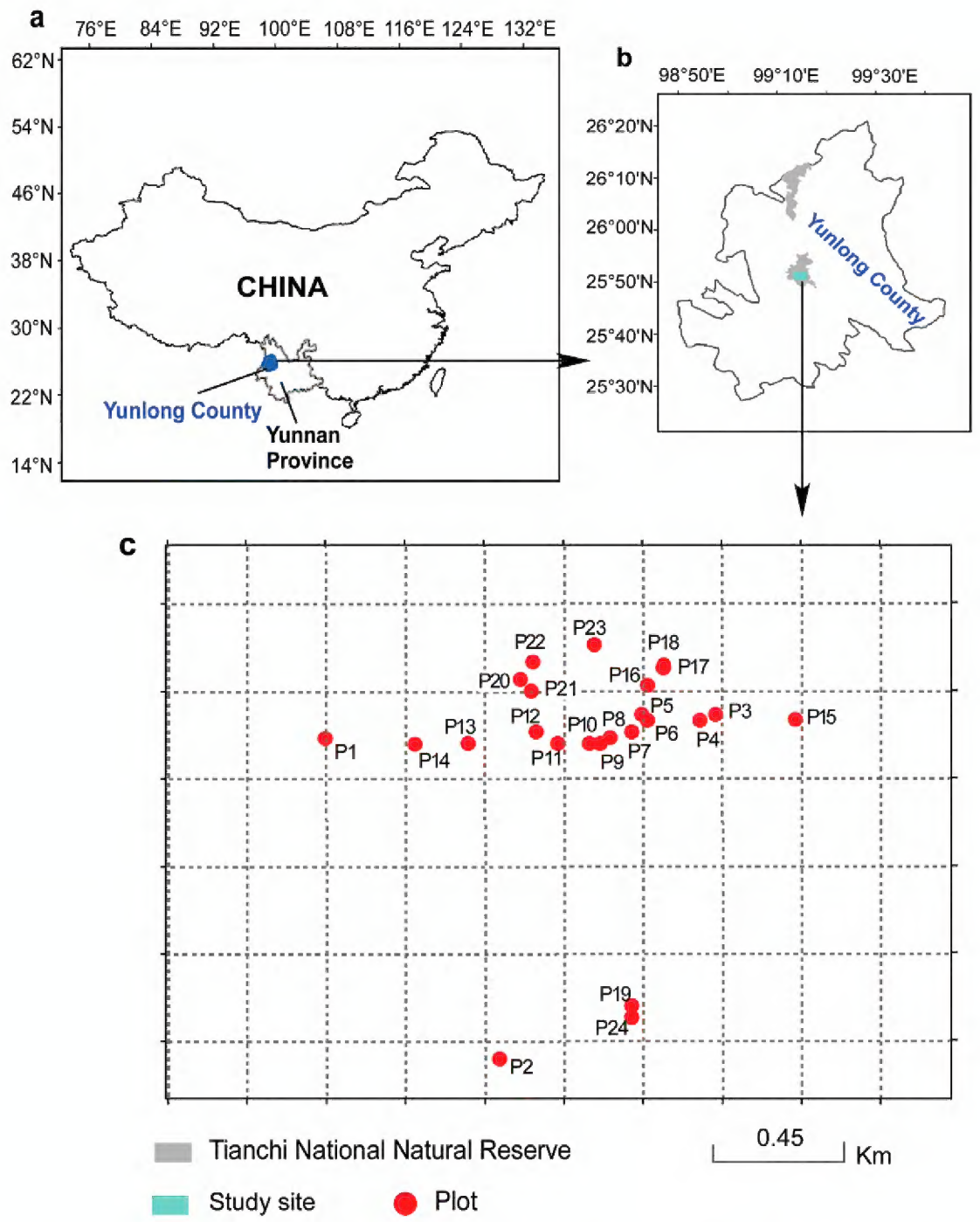

Figure 1. The study area. (a) Yunlong County in northwestern Yunnan. (b) The Tianchi National Nature Reserve in Yunlong County. (c) Plots located in the Tianchi National Nature Reserve.

maturing to brown or chestnut brown. Seeds with membranous wings are anemophilous (wind-dispersed). *P. yunnanensis* is a light-demanding species. It appears to be drought resistant, but requires forest gaps or disturbances to regenerate. Its distribution center is located on the plateau of Yunnan, also extending east into western Guizhou, northeast into western and southwestern Sichuan, south into southern Yunnan, southeast into western Guangxi, and northwest into southeastern Tibet, China.

Data collection and analysis

The forests in the study area are subjected to a range of natural and anthropogenic factors (such as elevations, topography, natural disturbances and human activities) thus, are structurally and floristically heterogeneous and the landscape pattern of vegetation is small mosaic patches. We selected plots in each patch containing *P. yunnanensis* in the study area. During July-August 2017, we established 24 plots containing *P. yunnanensis* between 2,530 and 3,100 m in this specific area of the Reserve (25°49'48"–25°57'70"N, 99°13'14"–99°20'34"E) (Figure 1c). The plots were established in the locations depending on access. The plot size varied between 20 m × 20 m to 40 m × 30 m where plot size depended on the size of the patch. Patch size was determined by species composition and topographic similarity. General information was noted including slope positions, altitude, slope exposure, slope inclination, and disturbance history.

Tree stems were classified into four classes based on their vertical position, crown position, and height: emergent layer ($H \geq 28$ m tall), canopy ($20 \text{ m} \leq H < 28$ m tall), subcanopy ($8 \text{ m} \leq H < 20$ m tall), and shrub layer ($1.3 \text{ m} \leq H < 8$ m tall). For all individuals greater than 1.3 m tall, DBH was used to calculate basal area and then basal area (BA) for each species found in a plot could be determined.

Understory woody species less than 1.3 m tall were divided into two classes: (1) $5 \text{ cm} \leq H < 50$ cm tall for seedlings and (2) $50 \text{ cm} \leq H < 130$ cm for saplings. Within these two classes, each individual was identified, counted, and measured for height and percentage foliage cover. For the species in each plot, all individuals at least 1.3 m in height were identified to species level, numbered and tagged, noted whether healthy, unhealthy, or dead.

We obtained 71 increment cores from *P. yunnanensis* trees of varying DBHs in the study area. For each tree trunk, a single increment core was taken from at 1 m above ground level. The length of time from the position at 1 m in height to ground level was estimated to be nine years

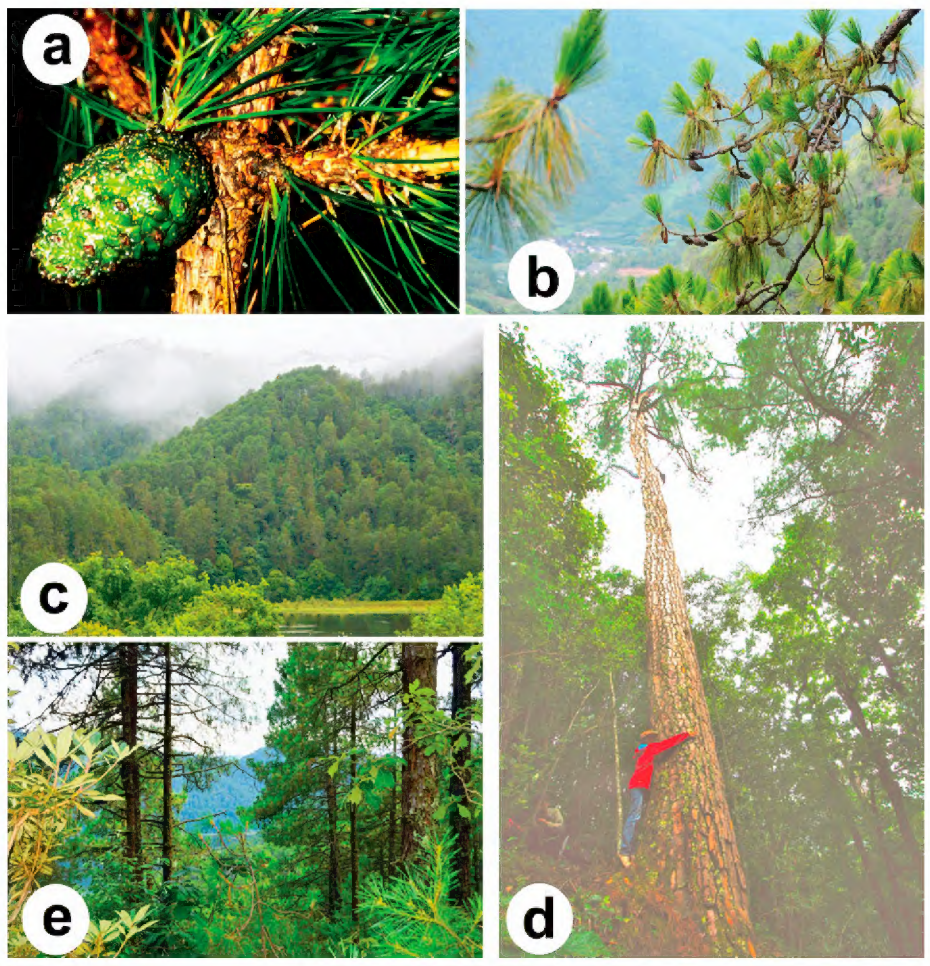

Figure 2. *Pinus yunnanensis* and its forest in the Tianchi National Nature Reserve. (a) Three needles per bundle and a seed cone of *P. yunnanensis*. (b) Branches with foliage and seed cones of *P. yunnanensis*. (c) The *P. yunnanensis* forest. (d) A *P. yunnanensis* tree with 33 m tall and 116 cm DBH. (e) Saplings of *P. yunnanensis* in a canopy gap.

based on field observations. The nine years was added to the data of ages we obtained from each increment core. For comparison, we also obtained 61 increment cores of *P. yunnanensis* from naturally regenerated secondary forests of Kunming and Yongren, central Yunnan. Tree age was determined using the software WinDENRO tree ring analysis system. From this analysis, we were also able to determine ring widths and to calculate basal area increments (BAI). The following formula was used to calculate BAI: X-(X-1) where X is the basal area at year X (last year of growth) and X-1 is the basal area of the tree measured up to the year previous to X. BAI is used in forest growth studies because it accurately quantifies wood production based on the ever-increasing diameter of a growing tree (Rubino and McCarthy 2000).

In each plot, the relative basal area (RBA, %) of each species was used as a measure of abundance of the species. Plant communities were classified using a floristic similarity dendrogram with Relative Sørensen and Group Average clustering [PCORD software (McCune and Mefford 1999)].

Dominance was determined using a dominance analysis according to the RBA of each species (Ohsawa 1984). The communities were named according to dominant species.

Diversity was calculated for each forest stand using species richness (number of species), the Shannon-Wiener's diversity index (Shannon-Wiener index) (Pielou 1969) and Simpson's diversity index (Simpson index) (Lande 1996). The measurement unit bit (logarithm bases 2) for Shannon-Wiener index was used. The proportion of total number of individuals was applied for calculating the diversity indices. Differences in species richness and diversity indices among habitats were analyzed by the non-parametric Kruskal-Wallis all-pairwise comparisons test, using Analyze-it Software (https://analyse-it.com; 2009). In order to examine tree growth in *P. yunnanensis* over time across all age classes both ring width (mm) and BAI (mm^2) were used.

Results

Forest types, stratification and species diversity

From our 2017 vegetation study, six distinct forest communities (at the 62% floristic similarity threshold) were classified according to the floristic similarity dendrogram (Figure 3a). These were: (1) Type 1: coniferous *P. yunnanensis* forest distributed in valley bottoms, slopes and ridges at elevations of 2,570–2,990 m; (2) Type 2: coniferous *P. yunnanensis* and evergreen broad-leaved *Lithocarpus variolosus* mixed forest distributed in mid slopes at elevations 2,680–2,760 m; (3) Type 3: coniferous *P. yunnanensis* and deciduous broad-leaved *Quercus griffithii* mixed forest distributed in lower slope positions at elevations 2,530–2,550 m; (4) Type 4: evergreen broad-leaved and coniferous mixed forest *Castanopsis orthacantha-P. yunnanensis-Schima argentea* distributed in valleys at elevations 2,570–2,600 m; (5) Type 5: coniferous, evergreen and deciduous broad-leaved mixed forest *P. yunnanensis-Schima argentea-Quercus griffithii* distributed in lower and mid slopes at elevations 2,530–2,890 m; (6) Type 6: coniferous and sclerophyllous evergreen broad-leaved mixed forest *P. armandii-Quercus rehderiana-P. yunnanensis* distributed in upper slopes and ridges at elevations 3,040–3,100 m.

The landscape pattern of these six forest types in the Tianchi area was a mosaic determined by elevation and topography as well as various natural and anthropogenic disturbances. *P. yunnanensis* is consistently one of the dominants in each of these six forest types. In forest Type 1 the disturbance histories were diverse and included landslides, cattle and goat browsing, evidence of lightning strike on older trees. In contrast, disturbance histories for the other five forest types mainly consisted of landslides. Additionally, there was evidence of selective cutting and other human activity (such as collecting leaf litter) in the forest understory in Type 2 and Type 3 forests.

Figure 3b depicts the stratification of *P. yunnanensis* with each of the six forest types. In Type 1, *P. yunnanensis* dominated the canopy (20–28 m) and subcanopy (8–20 m) layers. It reached 35 m in height in the emergent layer. In addition, many *P. yunnanensis* individuals were found in the shrub layer. This is a typical primary mature forest of *P. yunnanensis*. A few trees of *Lithocarpus craibianus* and *Schima argentea* were present in the canopy and subcanopy layers. *Alnus nepalensis* and *Quercus griffithii* were found along the forest edge. In the shrub layer, *Lyonia ovalifolia* and *Sorbus folgneri* are the main members.

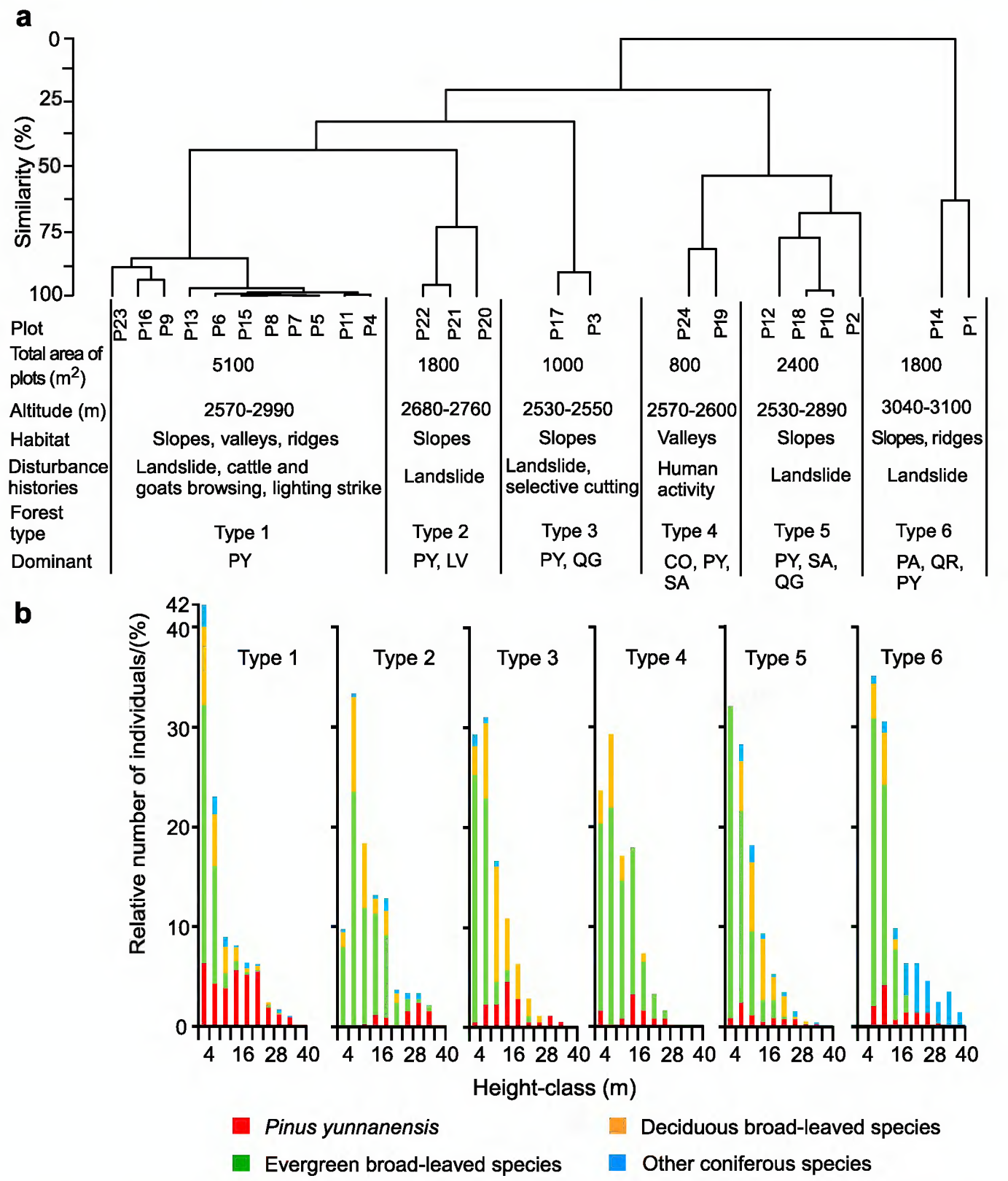

Figure 3. Floristic dendrogram and habitat characteristics, as well as forest stratification. (a) Floristic similarity dendrogram and habitat characteristics. (b) Height-class frequency distribution of species (height ≥ 1.3 m). Abbreviations for (a): PY = *Pinus yunnanensis*; LV = *Lithocarpus variolosus*; QG = *Quercus griffithii*; CO = *Castanopsis orthacantha*; SA = *Schima argentea*; PA = *Pinus armandii*; QR = *Quercus rehderiana*.

In Type 2, *P. yunnaensis* reached both the emergent layer (28–35 m) and the canopy, but only a few were found in the subcanopy and none between 1.3–12 m. *Lithocarpus variolosus* and *Pinus armandii*, *Cyclobalanopsis oxyodon* were found in the subcanopy and shrub layers.

In Types 3 and 4, the maximum height of *P. yunnaensis* also reached 35 m in the emergent layer. In Type 3, *P. yunnaensis* and *Quercus griffithii* shared the canopy and subcanopy. In Type 4, *Castanopsis orthacantha, P. yunnanensis* and *Schima argentea* co-occupied the canopy and subcanopy. In Type 5, *P. yunnanensis, Schima argentea* and *Quercus griffithii* co-dominated the canopy, subcanopy and shrub layers.

Type 6 is found above 3,000 m (3,040–3,100 m). Two pine species, *P. armandii* and *P. yunnanensis*, occupied the canopy layer, while in the emergent layer only *P. armandii* reached 38 m tall. Sclerophyllous evergreen broad-leaved *Quercus rehderiana* shared the subcanopy with the two pine species. In the shrub layer, *Rhododendron delavayi*, *Lyonia ovalifolia*, *Viburnum cylindricum* were common. In forest Types 3, 4, 5 and 6, there were fewer individuals of *P. yunnanensis* in the shrub layer than that of *P. yunnanensis* in the shrub layer of Type 1. The emergent layer of each forest type was made up of light-demanding, long-lived species (i.e. *P. yunnanensis* in the first four forest types, and *P. armandii* in the last two forest types).

The floristic composition of woody species in the six forest types is shown in Table 1. In total, 68 woody species comprised of 3 coniferous, 37 evergreen broad-leaved and 28 deciduous broad-leaved species belonging to 47 genera in 26 families were recorded in the 24 plots (Table 1 and Suppl. material 1). While the plots pooled for each forest type, 48 and 33 woody species were found respectively in Type 1 *P. yunnanensis* forest and Type 5 *P. yunnanensis-Schima argentea-Quercus griffithii* forest. In contrast, fewer than 25 woody species were found in each of the oth-

Table 1. Floristic composition of woody species (height ≥ 1.3 m) in the six forest types. The relative basal area in % is given. Background shading indicates dominant species. PY = *Pinus yunnanensis*; LV = *Lithocarpus variolosus*; QG = *Quercus griffithii*; CO = *Castanopsis orthacantha*; SA = *Schima argentea*; PA = *Pinus armandii*; QR = *Quercus rehderiana*.

Forest type	**Type 1**	**Type 2**	**Type 3**	**Type 4**	**Type 5**	**Type 6**
Dominant species	PY	PY, LV	PY, QG	CO, PY, SA	PY, SA, QG	PA, QR, PY
Range of elevation (m)	2570-2990	2680-2764	2530-2546	2576-2583	2530-2890	3042-3100
Number of plots	11	3	2	2	4	2
Total area of plots (m^2)	5100	1800	1000	800	2400	1800
Coniferous						
Pinus yunnanensis	74.37	43.91	49.88	23.66	34.41	17.05
Pinus armandii	4.58	10.49	0.6		6.63	53.06
Tsuga dumosa	0.03	·	·	·	0.51	0.05
Evergreen broad-leaved						
Lithocarpus variolosus	1.87	23.76	·	·	·	·
Rhododendron irroratum	1.42	·	0.63	0.25	1.61	0.68
Schima argentea	1.06	·	1.93	20.67	30.89	·
Lithocarpus craibianus	0.64	·	·	6.87	2.45	0.94
Rhododendron delavayi	0.53	1.15	1.43	0.22	1.94	2.79
Lyonia ovalifolia	0.32	0.3	1.46	0.12	0.12	0.2
Quercus rehderiana	0.26	·	0.02	·	0.08	20
Rhododendron basilicum	0.23	·	2.23	·	·	·
Viburnum cylindricum	0.18	0.35	0.17	0.01	0.09	0.05
Pieris formosa	0.14	·	·	·	0.09	1.16
Cornus capitata	0.05	0.79	·	·	0.5	·
Eurya nitida	0.05	2.03	·	0.25	·	·
Rhododendron decorum	0.02	1.93	·	·	·	·
Schefflera shweliensis	0.02	·	·	·	0.02	0.02
Cotoneaster franchetii	0.01	·	·	0.001	·	
Gaultheria fragrantissima	0.01	·	·	·	0.01	·
Symplocos lucida	0.01	·	0.05	·	0.001	·
Acanthopanax evodiaefolius var. *gracilis*	0.001	0.23	·	·	0.001	0.05
Daphne papyracea	0.001	·	·	·	·	0.03
Ternstroemia gymnanthera	0.001	·	·	·	·	·
Rhododendron tanastylum	0.001	·	·	·	·	·
Litsea yunnanensis	0.001	·	·	·	·	·
Cyclobalanopsis oxyodon	·	4.4	·	·	·	·
Machilus longipedicellata	·	0.41	·	·	·	·
Quercus guajavifolia	·	0.36	·	·	·	·
Illicium simonsii	·	0.05	·	·	·	·
Ilex dipyrena	·	0.01	·	·	·	·
Castanopsis orthacantha	·	·	·	37.47	·	·
Symplocos sp.	·	·	·	6.19	1.47	·
Ilex cornuta	·	·	·	·	0.01	·
Quercus aquifolioides	·	·	·	·	·	2.89
Deciduous broad-leaved						
Alnus nepalensis	5.78	·	0.22	·	1.89	·
Quercus griffithii	5.47	3.63	38.71	0.07	11.17	0.001
Cerasus clarofolia	1.48	0.18	2.14	1.56	1.89	·
Acer davidii	0.7	·	0.01	0.04	0.77	0.61
Populus davidiana	0.4	0.87	0.07	·	0.93	0.08
Schisandra sphenanthera	0.14	·	0.44	·	·	·
Sorbus folgneri	0.06	0.001	·	0.13	0.03	0.03
Enkianthus quinqueflorus	0.05	·	·	·	0.9	0.16
Litsea pungens	0.02	·	·	0.47	·	·
Elaeagnus umbellata	0.01	·	·	·	·	·
Betula insignis	0.01	·	·	·	·	·
Toxicodendron succedaneum	0.01	·	·	·	·	·
Pyrus xerophila	0.01	·	·	·	·	·
Coriaria nepalensis	0.01	·	·	·	·	·
Hypericum sp.	0.01	·	·	·	·	·
Rosa macrophylla	0.01	·	·	·	·	·
Berberis diaphana	0.001	·	0.001	·	0.01	·
Rosa sp.	0.001	·	·	0.001	·	·
Cotoneaster acuminatus	0.001	·	·	·	·	0.01
Rubus stans	0.001	·	·	·	·	0.001
Rosa multiflora	0.001	·	·	·	·	·
Viburnum betulifolium	0.001	·	·	·	·	·
Betula alnoides	·	2.5	·	·	·	·
Sorbus vilmorinii	·	2.03	·	·	·	0.01
Rhododendron yunnanense	·	0.61	·	·	·	·
Decaisnea insignis	·	0.01	·	·	·	·
Salix matsudana	·	·	·	1.98	0.98	·
Zanthoxylum simulans	·	·	·	0.05	·	·
Rubus hypopitys	·	·	·	·	0.51	·
Symplocos paniculata	·	·	·	·	0.3	·
Hydrangea macrophylla	·	·	·	·	0.08	·
Ligustrum quihoui	·	·	·	·	0.01	·
Padus obtusata	·	·	·	·	0.001	·
Acer oliverianum	·	·	·	·	0.001	0.11

er four forest types (Types 2, 3, 4 and 6) (Figure 4a). However, species richness (average number of species among the plots of each forest type) was not significantly different among all the forest types (Figure 4b). Among the six forest types, diversity indices (ranging from 1.9–2.3 for the Shannon-Wiener index, 0.75–0.86 for the Simpson index) were not significantly different (Figures 4c, d).

Stand structure and regeneration

Diameters of cored trees ranged between 2–116 cm and ages ranged between 11–172 years old. Diameter and age were significantly correlated (Figure 5, $R^2 = 0.86$).

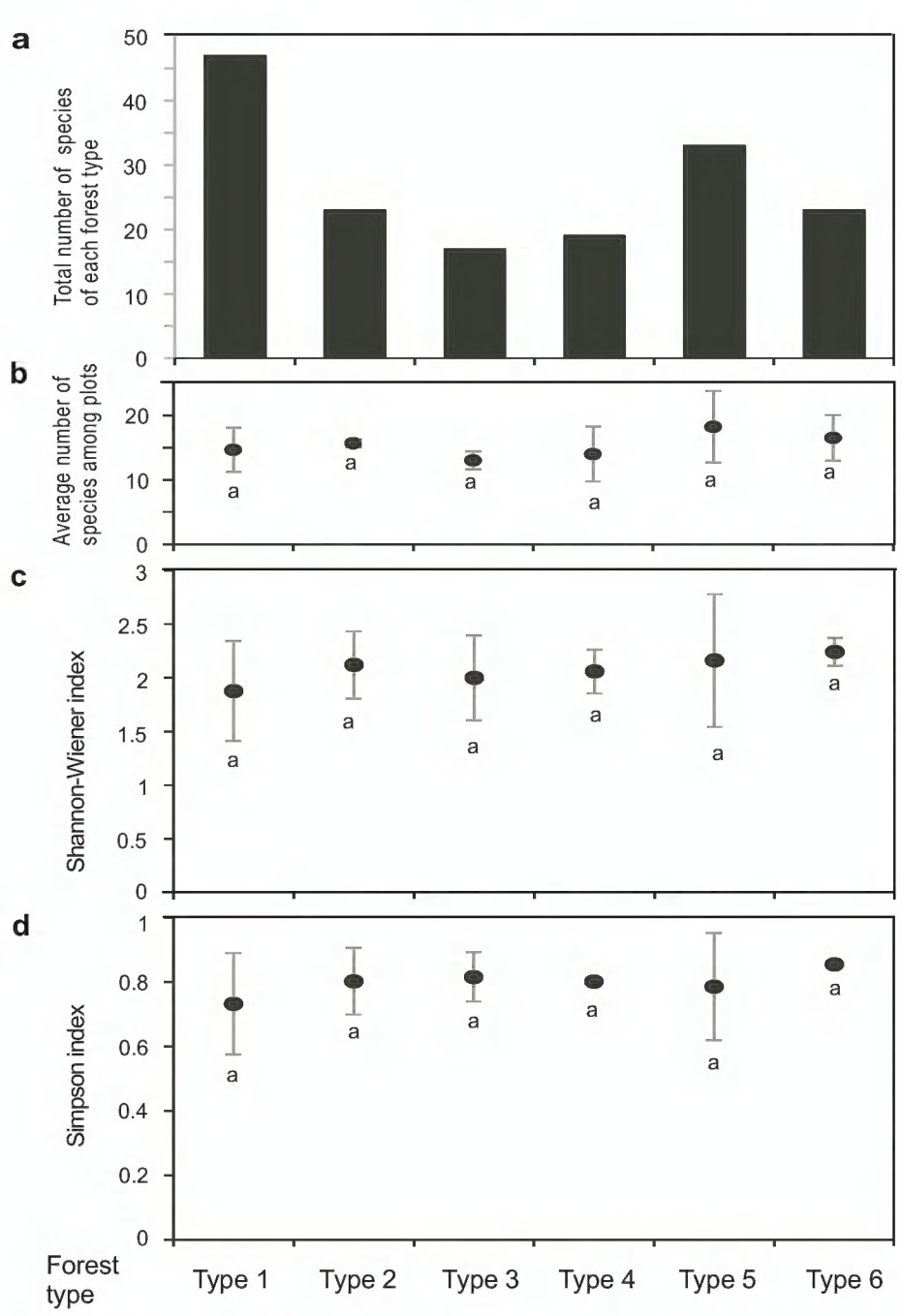

Figure 4. Changes in species richness and diversity among the six forest types. (a) Total number of species of plots of each forest type. (b) Average number of species among plots of each forest type. (c) Shannon-Wiener index. (d) Simpson index. Forests sharing the same letters do not differ significantly by non-parametric Kruskal-Wallis all-pairwise comparisons test, $P < 0.05$. The bar indicates the standard deviation. Forest types: Type 1 = *Pinus yunnanensis* forest; Type 2 = *Pinus yunnanensis-Lithocarpus variolosus* forest; Type 3 = *Pinus yunnanensis-Quercus griffithii* forest; Type 4 = *Castanopsis orthacantha-Pinus yunnanensis-Schima argentea* forest; Type 5 = *Pinus yunnanensis-Schima argentea-Quercus griffithii* forest; Type 6 = *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* forest.

Diameter size-class frequency distributions of *P. yunnanensis* and other co-dominant tree species in all six forest types are shown in Figure 6. In the monodominant *P. yunnanensis* forest (Type 1), five height classes of *P. yunnanensis* corresponded to five peaks in the diameter distribution, indicating sporadic regeneration. But among the peaks, the four highest peaks appeared in the very small DBH classes (0–20 cm), the last peak being in 30–35 cm DBH. The five sub-populations were found in open patches, which provided some direct sunlight to the light demanding *P. yunnanensis* saplings and young trees on the forest floor. A large number, 251, of well-established seedlings/saplings (20–128 cm in height) of *P. yunnanensis* and a very few (5–16) seedlings/saplings of other canopy tree species were found in canopy gaps and forest edges.

In the *P. yunnanensis-Lithocarpus variolosum* forest (Type 2), the two dominants also showed a sporadic pattern of regeneration. There were no young trees (less than 5 cm DBH) of either *P. yunnanensis* or *L. variolosum,* because the evergreen *L. variolosum* crowns in the subcanopy layer allowed very little sunlight to reach the forest floor, resulting in poor regeneration of the two species.

In the *P. yunnanensis-Quercus griffithii* forest (Type 3), the two dominant species showed sporadic regeneration. Two *P. yunnanensis* and five *Quercus griffithii* trees were found between 100–125 cm and 30–75 cm DBH, and trees between 5–25 cm DBH were not abundant. Deciduous *Quercus griffithii* had four peaks within the DBH-classes of 10–40 cm.

In the *Castanopsis orthacantha-P. yunnanensis-Schima argentea* forest (Type 4), all the three dominant species showed sporadic regeneration. The dominants *C. orthacantha*, *P. yunnanensis* and *S. argentea*'s maximum diameters reached only 55, 50 and 45 cm DBH, respectively. In Type 3 and Type 4 forests, which are found at the low elevations (2,530–2,590 m), human impact was evident, as open spaces left after selective tree felling for timber during previous decades.

In the *P. yunnanensis-Quercus griffithii-Schima argentea* forest (Type 5), *P. yunnanensis* and *Q. griffithii* had sporadic regeneration while *S. argentea* showed an inverse-J shaped

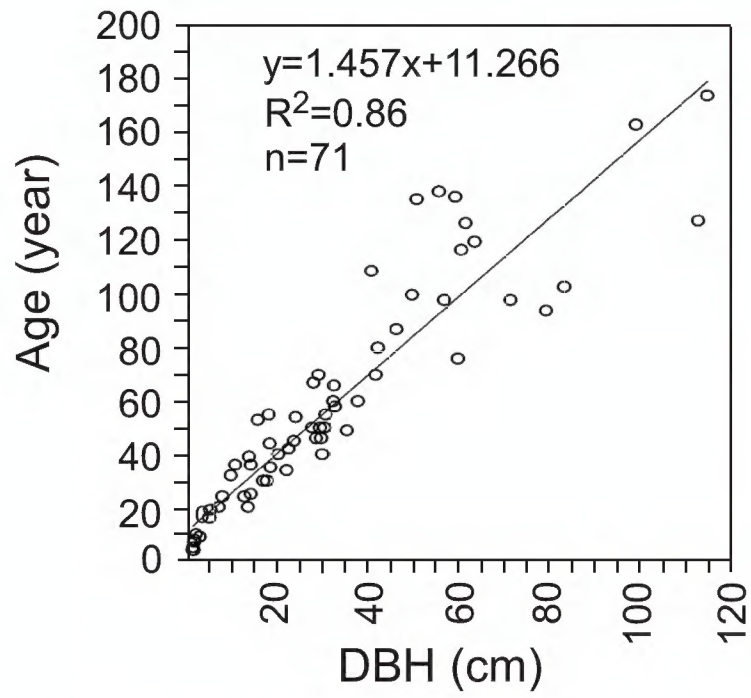

Figure 5. Relationships of age and DBH.

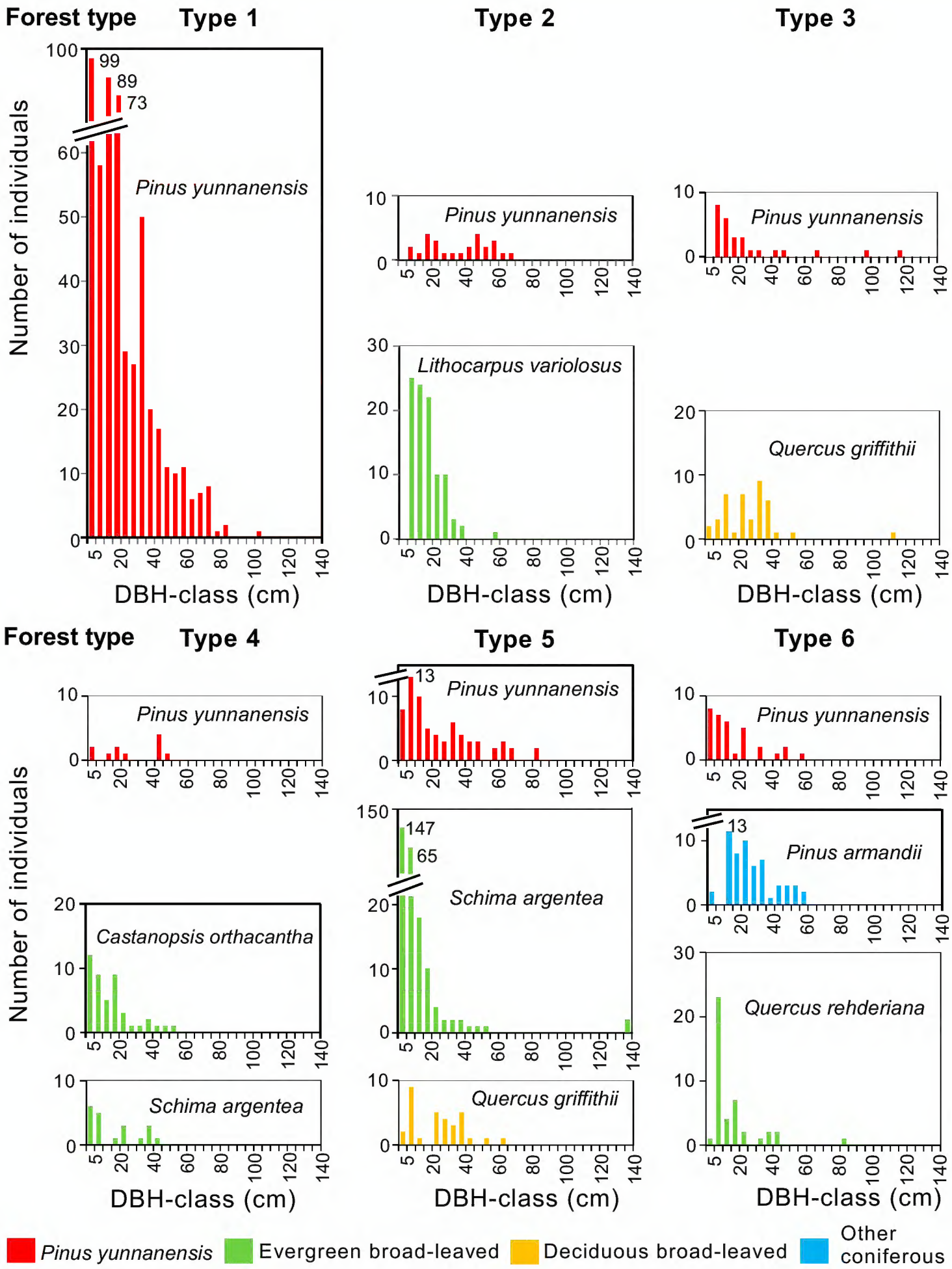

Figure 6. DBH-class frequency distribution of dominant species in various forest types. Type 1 = *Pinus yunnanensis* forest; Type 2 = *Pinus yunnanensis-Lithocarpus variolosus* forest; Type 3 = *Pinus yunnanensis-Quercus griffithii* forest; Type 4 = *Castanopsis orthacantha-Pinus yunnanensis-Schima argentea* forest; Type 5 = *Pinus yunnanensis-Schima argentea-Quercus griffithii* forest; Type 6 = *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* forest.

pattern indicating a very active and recent pattern of regeneration. In this forest type, one tree of *P. yunnanensis* reached 90 cm DBH while two trees of *S. argentea* reached 130–140 cm DBH. *Q. griffithii*'s DBH ranged 0–60 cm.

In the *P. armandii-P. yunnanensis-Quercus rehderiana* forest (Type 6) at the highest elevations (3,040–3,100 m), the three dominant species all showed a sporadic pattern of regeneration. They had peaks at 15–20 (for *P. armandii*), 0–5 (*P. yunnanensis*) and 5–10 (*Q. reheriana*) cm DBH-classes. While the two pine species reached 60 cm DBH, *Q. reheriana* reached 85 cm DBH. Young trees and saplings of *Q. reheriana* appear both under canopy trees and in open spaces suggesting a somewhat shade-tolerant species in contrast to the two shade-intolerant pine species.

A few well-established seedlings/saplings (fewer than 30) of either *P. yunnanensis* or other canopy tree species were found in Types 2–6.

As a whole, there has been a relatively steady recruitment of *P. yunnanensis* trees over time peaking some 15 to 30 years ago. Although for trees taller than 1.3 m, there appears to be fewer trees in the period between 2002 and

2017 (the most recent age class), the seedling data (251 well-established seedlings/saplings) suggest that the regeneration has been good since 2002.

Growth rate and age-structure

Diameter growth of trees can be estimated by ring width and basal area increment. Changes in either may indicate increases or decreases in growth. The growth rate among the 71 samples varied greatly. In general, when the trees were less than 10 years old, the average growth rate of radius (ring width) was relatively high, with 4.04 mm/year, ranging from 5.56 to 2.97 mm/year. Thereafter, the average rate of radial growth fell to 2.50 mm/year between ages 20–30 years, and 1.63 mm/year between 31–60 years, and 1.17 mm/year for trees 61–100 years old. For trees greater than 100 years old, the average growth rate was 0.55 mm/year. At the other extreme, the rate of height growth slowed within the first 10 years (data not shown). It took about nine years on average to reach 1 m tall. Trees in all the four age classes (0–40 years, 40–80 years, 80–120 years, 120–164 years) had a similar pattern to that ring widths started high and decreased in a reverse J-shape (Figure 7a)

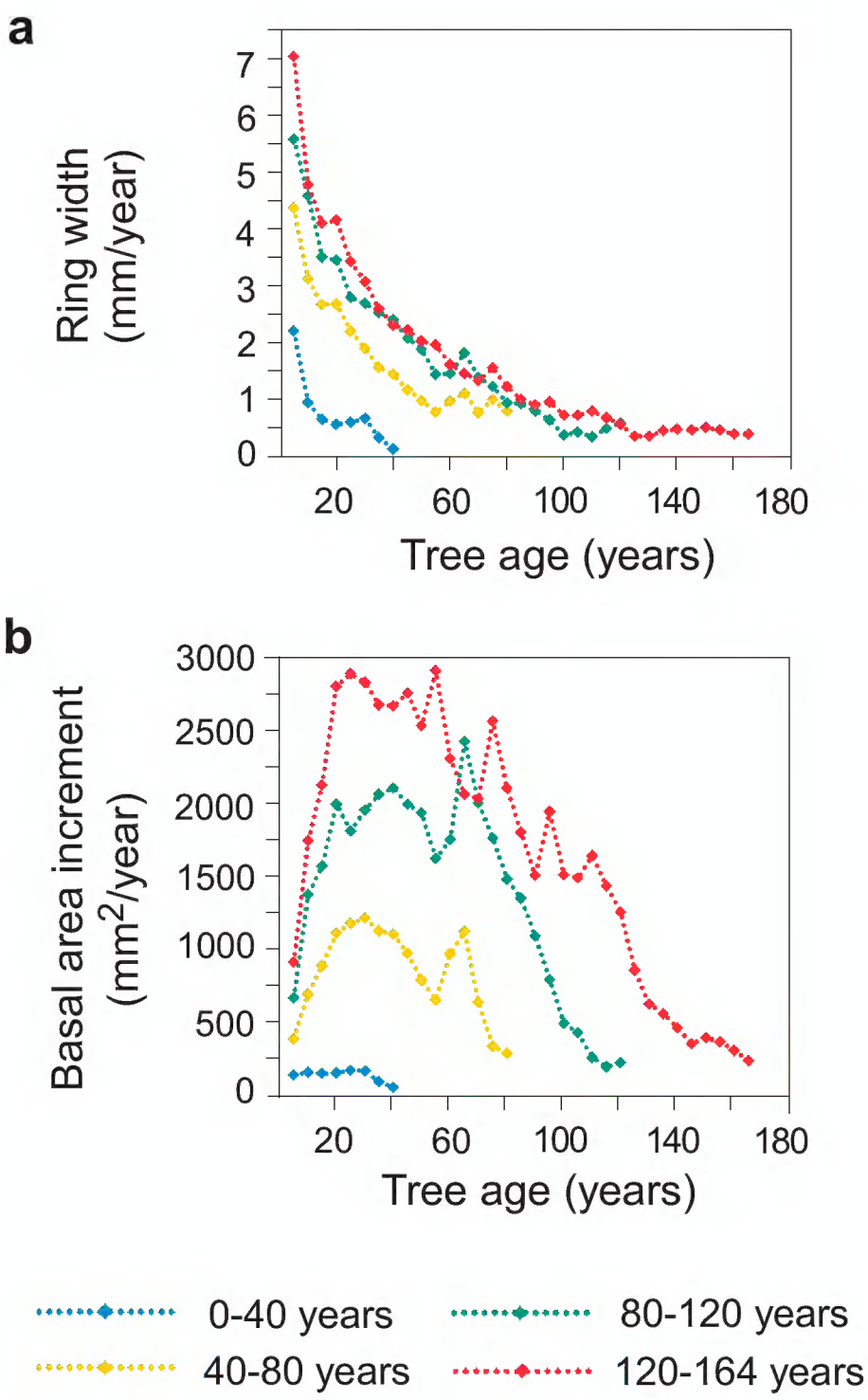

Figure 7. Growth trends of *Pinus yunnanensis* of the Tianchi National Nature Reserve. (a) The basal area increment for trees in the four age classes (i.e., 0–40, 40–80, 80–120, 120–164 years). (b) The ring width for trees in the four age classes.

P. yunnanensis trees exhibited basal area increments (BAI) that rapidly increased with age for the first 20 years in all trees older than 40 years (Figure 7b). In trees younger than 40 years, BAI gradually increased during the first 10 years, then the level remained roughly the same until age 30 years, and decreased between ages 30–40 years. For trees with an age greater than 80 years, BAI plateaued between age 20 and 30 years and maintained that plateau until between 70 and 80 years old at which point BAI in all trees declined (Figure 7b).

Moreover, *P. yunnanensis* trees in the older age classes grew faster during the first 40 to 80 years than younger trees at the same age. In other words, trees of *P. yunnanensis* generally grew faster during the period 1853–1897 (red line) than 1897–1937 (green line) than 1937–1977 (yellow line) than during 1977–2017 (blue line) in the Tianchi area (Figures 7a, b).

Figure 8 shows the age-structure of *P. yunnanensis* in various forests. The observed maximum age of *P. yunnanensis* was at least 105 years in all the forest types except Type 4. In the Type 1 forest, there were many *P. yunnanensis* presented in the young to middle age-classes. The oldest tree was 135-years; most trees were between 15 and 30 years old. The other two sub-peaks were at 30–60 years. Recruitments were in a sporadic pattern corresponding to their frequency distribution in DBH-classes (Figure 6). In canopy gaps and forest edges, 251 seedlings/saplings over four-years-old but younger than 12 years were found (data are not shown). In the Type 2 forest, tree ages ranged from 16 to 120 years, and no trees less than 15-year-old were found, suggesting that regeneration was not occurring. *P. yunnanensis* in Types 3 and 4 was discontinuously distributed in the age-classes. While *P. yunnanensis* in Type 3 reached 165 years, there were none less than 15 years old. Only eight established seedlings/saplings of *P. yunnanensis* were found in canopy gaps and forest edges. In Types 5 and 6, the forest ages reached 135 and 105 years, respectively. The numbers of *P. yunnanensis* trees in these two forest types show three very small peaks between 15–60 years but poor recruitment in age-classes of less than 15 years. As a whole in the age class data for all the forest types, *P. yunnanensis*' presence of young and old individuals indicates frequent regeneration as well as dominance at maturity in the Tianchi area. The Type 1 forest appeared to have the most frequent episodes of regeneration.

Discussion

Ecological traits and forest characteristics

P. yunnanensis is a light-demanding species with wind-dispersed seed that depends upon canopy gaps or disturbances for regeneration. It can mono-dominate a forest or co-dominate with diverse species in various mixed

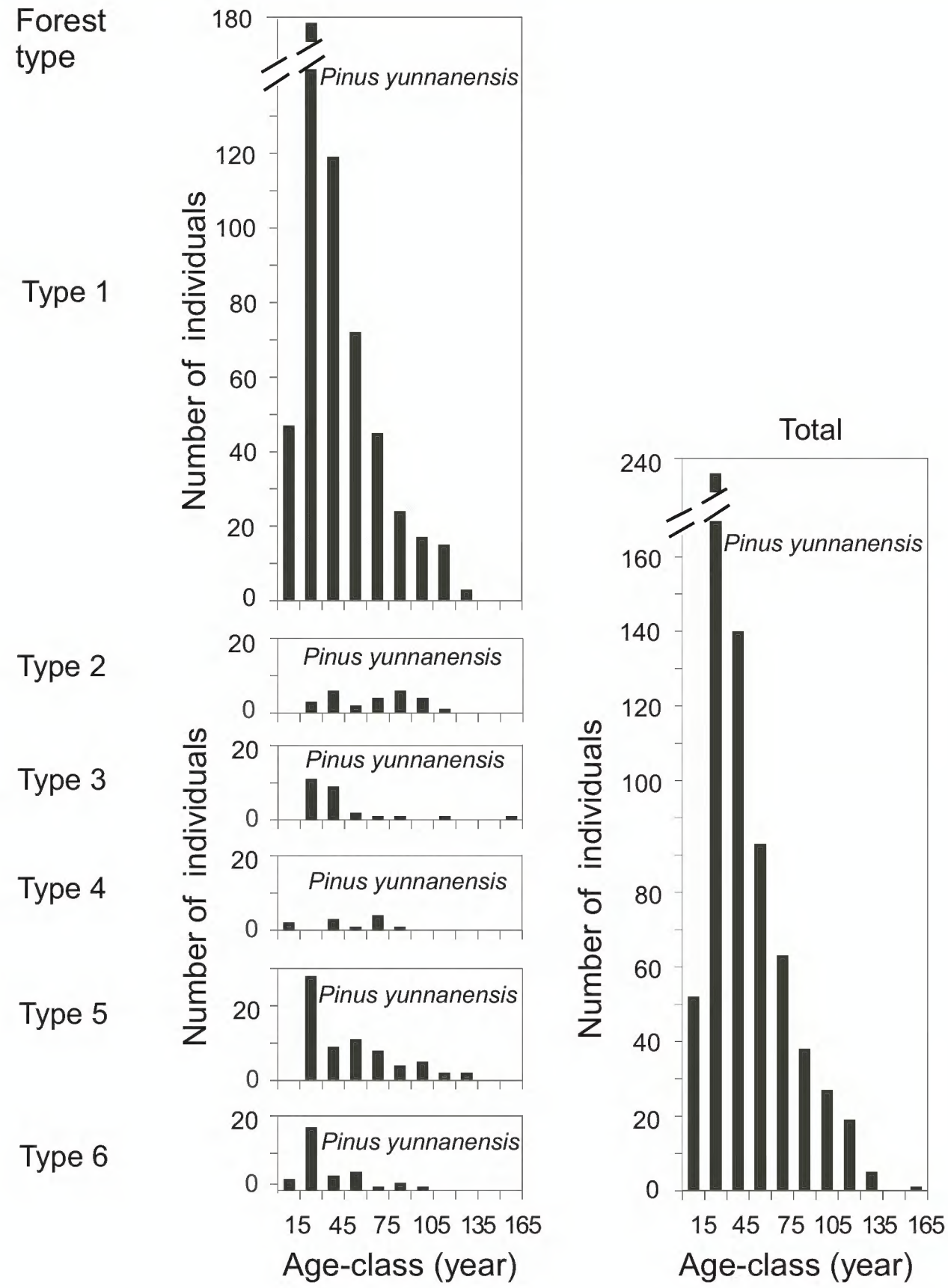

Figure 8. Age frequency distribution of *Pinus yunnanensis* in the six forest types. Forest type 1 = *Pinus yunnanensis* forest; Forest type 2 = *Pinus yunnanensis-Lithocarpus variolosus* forest; Forest type 3 = *Pinus yunnanensis-Quercus griffithii* forest; Forest type 4 = *Castanopsis orthacantha-Pinus yunnanensis-Schima argentea* forest; Forest type 5 = *Pinus yunnanensis-Schima argentea-Quercus griffithii* forest; Forest type 6 = *Pinus armandii-Quercus rehderiana-Pinus yunnanensis* forest.

forests. The overstory dominance of *P. yunnanensis* over a wide range of forest types and elevations suggests that this species plays an important role as an early successional species whose longevity assures presence in later successional stages. Among the evergreen broad-leaved trees (e.g. species of *Schima, Quercus, Castanopsis* and *Lithocarpus*) with which it co-occurs, it survives best on disturbed micro-sites or steep slopes (Figure 3a, Suppl.material 1). These ecological traits are very similar to those of *Pinus roxburghii* found in the Bhutan Himalaya (Wangda and Ohsawa 2006). Moreover, *P. roxburghii* is also associated with evergreen broad-leaved trees of *Quercus* (e.g. *Q. lanata*), the deciduous broad-leaved trees of *Quercus* (e.g. *Q. griffithii*) and shrubs of *Rhododendron* (e.g. *R. arboretum*), *Viburnum* (e.g. *Viburnum cylindricum*), *Lyonia* (e.g. *L. ovalifolia*), etc. In some of our study stands, *P. yunnanensis* co-dominates with deciduous broad-leaved *Q. griffithii* or coniferous *P. armandii*; similarly, its northern ecological partner *Pinus tabuliformis* is associated with deciduous broad-leaved trees of *Quercus aliena* var. *acutiserrata* and coniferous *P. armandii* in the Qinling Mountains, or *Quercus mongolica* (previous *Q. wutaishanica*) and *Betula platyphylla* in the Zhiwuling Mountains; *P. tabuliformis* is also shade-intolerant and its regeneration depends on disturbances (Yang et al. 2007; Wang et al. 2009; Lin 2009; Chai et al. 2012). In other of our study stands, *P. yunnanensis* co-dominates with evergreen broad-leaved *Schima argentea* and *Castanopsis orthacantha*; similarly, its southern ecological partner, also a pioneer and fast-growing pine tree, *P. kensiya* is associated with *Schima wallichii*

and species of *Castanopsis* including *Castanopsis hystrix*, *C. echidnocarpa*, *C. delavayi* and *C. calathiformis* (Li et al. 2013). *Pinus kensiya* occupies northern tropical and southern subtropical areas.

The Shannon-Wiener index of our study *P. yunnanensis* forest (1.9) tends to be higher than the natural mature *P. kensiya* forest (1.7) in the Ailao Mountains of central Yunnan (Song et al. 2011); and it is also higher than the secondary *P. yunnanensis* forests in Luquan (1.5) and Qiongzhusi (1.6), central Yunnan (Tang et al. 2010). All six study forest types had *P. yunnanensis* trees at least 90 years; these old-growth *P. yunnanensis* forests were stratified into multi-layers including emergent, canopy, subcanopy and shrub layers. In contrast, the 15–20 years old secondary *P. yunnanensis* forests of central Yunnan are simply composed of canopy and shrub layers. Often these forests are so dense that even the shrub layer is depauperate.

Recruitment patterns and growth trends

In the Tianchi National Nature Reserve of Yunnan, more seedlings/saplings were found in the Type 1, mono-dominant *P. yunnanensis* forest than in the mixed forest types (Types 2–6), because various disturbances including landslides, browsing, or lightning strike were noted in this forest type (Figure 3a). In the Tianchi area, seedlings/saplings of *P. yunnanensis* appear as uneven clusters. Seedling heights after the first four years following germination averaged only 6–10 cm. It then took another five years on average to reach 1 m in height. The initial height growth is slow as a result of competition for light as well as the allocation of carbon for root development; however, for seedlings growing in more open environments, such as along roadsides, height growth can be much greater taking between four to seven years to reach 1 m. The mortality of young seedlings is high during the first four years. This pattern of seedling growth and survival is similar to that observed with natural regeneration of plantations of *P. yunnanensis* of central Yunnan (Wang et al. 2017).

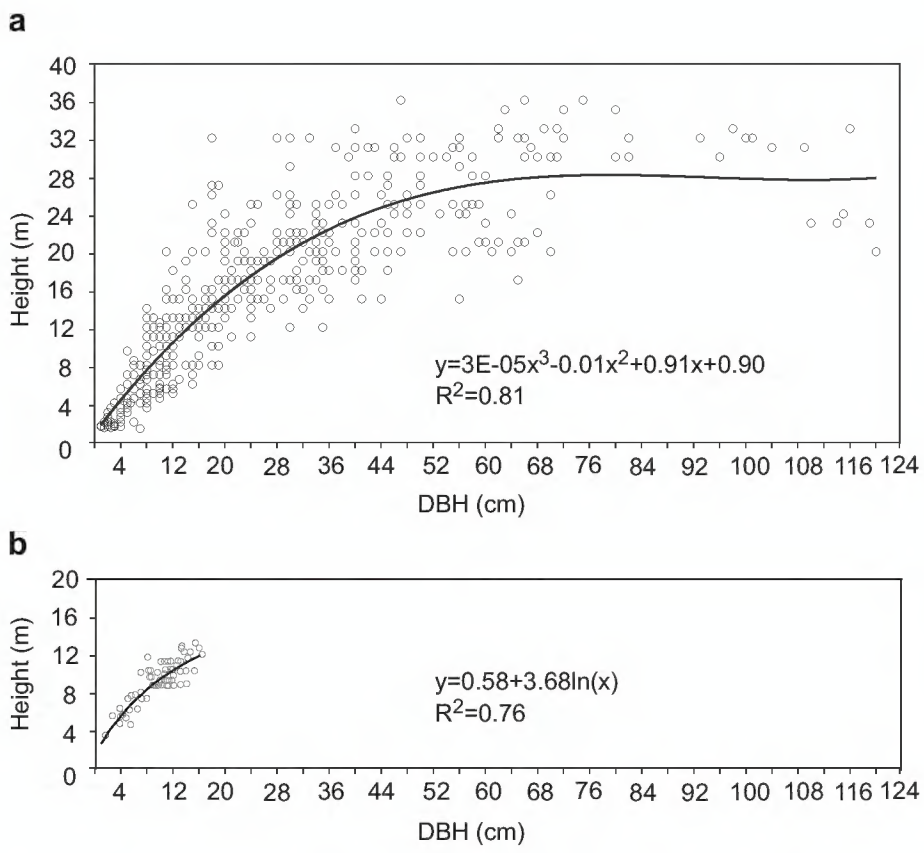

Figure 9. A comparison of relationships of DBH and height of *Pinus yunnanensis* between the old-growth forest of the Tianchi National Nature Reserve (a) and the 14 years-old *P. yunnanensis* plantation of Shiping, central Yunnan (b). Data source: Su et al. (2010) for (b).

After successful establishment, tree height of *P. yunnanensis* increases as DBH increases (Figure 9a). As the height approaches 24 m, the increase slows considerably. When trees of *P. yunnanensis* are smaller than 8 cm DBH, the height increase per year in the Tianchi area is similar to that of the plantation trees in Shiping, central Yunnan (Figure 9b). When both plantation and Tianchi trees are about 12 cm DBH, the Tianchi trees are 2 m taller than the plantation trees. The soil in Shiping is red earth and the climate is drier. Soil type significantly affects *P. yunnanensis* forests' species diversity and growth (Yang 2010). *P. yunnanensis* trees grow best in humid habitats with soils rich in nutrients (Jin and Peng 2004; Hu 2009). The humid habitat with yellow-brownish soil in the Tianchi area is more favorable for the growth of *P. yunnanensis*. Hu (2009) found a *P. yunnanensis* tree with a height of 56 m and a DBH of 86 cm in Baimalinchang of Yongren and it was 137-years-old. In contrast, Li et al. (2007) noted in a *P. yunnanensis* forest in Yongren, central Yunnan that there was a 257-year-old *P. yunnanensis* tree with a DBH of only 48 cm. This species can survive in very dry areas, generally with stunted and a crooked stature. The life span of *P. yunnanensis* growing on moderate to good sites may be around 180–280 years.

P. yunnanensis is a relatively fast-growing species in terms of tree ring width among the conifers of China. It attains a diameter of about 50 cm in 80 to 100 years, depending upon site quality. The patterns of ring width and basal area increment for *P. yunnanensis* trees growing in the Tianchi area where only site and time affected the patterns is shown in Figures 10a, d. In a secondary forest in central Yunnan where tree growth is impacted by site, time and human activity (such as extracting resin), the patterns of ring width and basal area increment are shown in Figures 10b and e. For both trees from the Tianchi forest and the secondary forest, ring widths started between 4 and 6 mm/yr and decreased in a reverse J-shaped pattern. A seemingly small difference in ring widths translates into very large differences in basal area increment (compare Figures 10d, e). For *P. yunnanensis* trees in a highly degraded forest in southwestern Sichuan, ring width showed a wave pattern (Hinckley et al. 2013). This wave pattern resulted from periodic branch removal interspersed by periods of crown recovery. Clearly, as site quality increases and human activity decreases, tree growth increases. The maximum basal area increment approached 1,500 mm^2 per year for trees at Tianchi whereas trees in the secondary forest of Yunnan and southwest Sichuan only approached 750 mm^2/yr.

As noted earlier, trees of the older age classes grew faster than younger trees at the same age in the Tianchi area (Figures 7a, b). This probably resulted from differences in

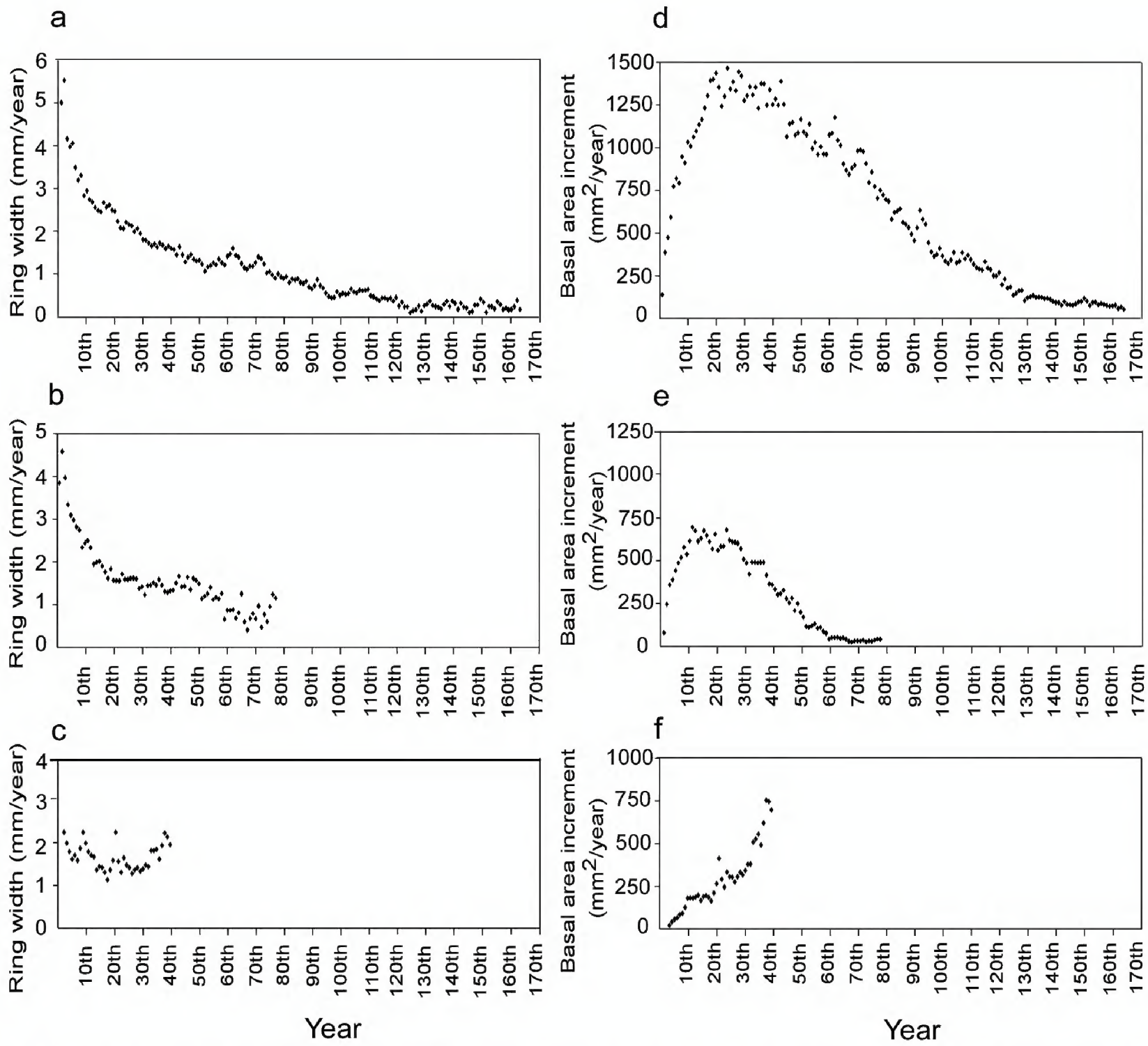

Figure 10. Comparisons of growth trends of *Pinus yunnanensis* among the old growth forest of the Tianchi National Nature Reserve (a & d), the secondary forest of central Yunnan (b & e), and the degraded forest under human pressure of western Sichuan (c & f). Data sources: Our own field work as seen this study for (a), (d), (b) and (e); Hinckley et al. (2013) for (c) and (f).

stand development such as the timing of canopy closure and the growth and development of competing species. It might also be resulted from differences in aspect where *P. yunnanensis*' light-demanding nature would result in better growth on southern versus northern slopes. Differences in disturbance regimes such as landslide frequencies and intensities also might have impacted the growth pattern. Finally, rapid global climate changes over many decades may be an additional important factor influencing growth. All the combined factors may lead to the observed differences.

Old-growth forests

The *P. yunnanensis* forests of the Tianchi area appear to be some of the last remnants of primeval and old-growth forests of this species. These forests are structurally diverse and contain a rich diversity of overstory, mid-story, and understory species. These forests also are valuable as a seed source and can serve as a genetic reservoir.

Author contributions

C.Q.T. designed the study, analyzed the data and wrote the manuscript. L.-Q.S. organized and analyzed the data. S.L. identified the botanical specimens. K.S. read the tree rings and provided the data of ring width. C.Q.T., L.-Q.S., P.-B.H., D.-S.H., Y.-F.L., Z.-Y.Z., L.-Y.Y., R.-H.Y. and H.-M.X. conducted the fieldwork. All the authors contributed discussion to improve the manuscript.

Acknowledgements

We acknowledge funding by the Science and Technology Ministry of China (2015FY210200-15) and the National Natural Science Foundation of China (31500355). We would like to thank all the staff of the management office of the Tianchi National Nature Reserve for allowing us to conduct field research in the reserve. Our sincere thanks go to Dr. Thomas M. Hinckley who provided valuable suggestions and comments to improve our manuscript.

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E-mail and ORCID

Cindy Q. Tang (Corresponding author, cindyqtang@aol.com), ORCID: https://orcid.org/0000-0003-3789-6771
Li-Qin Shen (liyilanbian@foxmail.com)
Peng-Bin Han (baqidehan@qq.com)
Diao-Shun Huang (1351379318@qq.com)
Shuaifeng Li (Corresponding author, 12704391@qq.com), ORCID: https://orcid.org/0000-0002-2555-1808
Yun-Fang Li (974016458@qq.com)
Kun Song (ksong@des.ecnu.edu.cn), ORCID: https://orcid.org/0000-0001-8019-9707
Zhi-Ying Zhang (zhyzhang@ynu.edu.cn)
Long-Yun Yin (409508296@qq.com)
Rui-He Yin (1318765303@qq.com)
Hui-Ming Xu (254134558@qq.com)

Supplementary material

Supplementary material 1
Floristic composition of woody species (height ≥ 1.3 m) in each plot
Link: https://doi.org/10.3897/VCS/2020/37980.suppl1